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SOME CONSEQUENCES OF DIFFUSE COMPETITION IN A DESERT ANT COMMUNITY

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MacArthur's (1972) broad definition of diffuse competition as "competition by a constellation of species" has permitted alternative interpretations and usages by ecologists. Pianka (1974) treated interactions with multiple competitors in a simple additive fashion. Consequently, unless niche overlaps were simultaneously reduced, an increase in the intensity of competition automatically attended enhanced species packing, and the persistence of species in a competitively structured community inevitably became more precarious. An obvious oversimplification of this view is the neglect of indirect pathways of competitive interaction in communities of three or more species (Levins 1975; Levine 1976). For example, consider a simple three-species system of resource-limited consumers in which species j and h compete moderately, and species i competes intensely with h but only slightly with j. Although the direct pairwise interaction between species i and j is competitive, in the context of the three-species community i may actually increase the population growth rate of species j by suppressing that of species h. If the indirect effects of competition outweigh the direct effects, the net interaction may be facilitative rather than competitive (Levine 1976), and the diffuse competition experienced by a particular competitor may actually decline with greater species packing. In this study I investigate the importance of indirect pathways of competition in the determination of diversity and structure in a community of harvester ants.

THE THEORY

Net interspecific interaction coefficients may be calculated for communities near equilibrium by solving the linear equations (Levins 1968) $A\hat{N} = K$ for species' equilibrium densities, giving $\hat{N} = A^{-1}K$, or

$$\begin{aligned} \hat{N}_i &= a^{-1}_{ii}K_i + a^{-1}_{ij}K_j + a^{-1}_{ih}K_h, \\ \hat{N}_j &= a^{-1}_{ji}K_i + a^{-1}_{jj}K_j + a^{-1}_{jh}K_h, \\ \hat{N}_h &= a^{-1}_{hi}K_i + a^{-1}_{hj}K_j + a^{-1}_{hh}K_h. \end{aligned} \tag{1}$$

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The inverse of the matrix of competition coefficients, A^{-1}, relates the vector $(\hat{N})$ of species' equilibrium densities to the vector (K) of species' carrying capacities. Off-diagonal elements, a_{ij}^{-1}, of this matrix thus represent $\partial\hat{N}_i/\partial K_j$, and these may be positive or negative depending on the relative values of the direct and indirect interaction terms that comprise each a_{ij}^{-1} (Levine 1976). The inverted competition matrix may be normalized by dividing each element of a column by its diagonal element a_{ii}^{-1}. In the normalized matrix, termed A' by Levine (1976), the diagonals are all unity, and a change in the magnitude of K_j sufficient to change $\hat{N}_j$ by $+1$ will change $\hat{N}_i$ by a'_{ij}, $\hat{N}_k$ by a'_{kj}, and so on. In a three-species community, the off-diagonals of this matrix take the form $(a_{ij}a_{hj} - a_{ij})/(1 - a_{ih}a_{hi})$, where $(a_{ij}a_{hj})/(1 - a_{ih}a_{hi})$ evaluates indirect interspecific interactions between species i and j.

THE PREDICTIONS

If the elements of the normalized inverse accurately represent the $\partial\hat{N}_i/\partial K_j$, they should be useful in anticipating correlations in species' abundances and population responses to manipulations in species' carrying capacities. For K_h varying independently, a significantly positive a'_{ih} $(\partial\hat{N}_i/\partial K_h)$ predicts that the abundances of species i and h will be positively correlated. Prediction is more complicated when several or all of the K's vary simultaneously, as is likely for the harvester ants studied here. Seed production occurs in response to periodic rainfall events, and reserves of all seed taxa are depleted by burial and granivory between production periods. When several K_h vary in unison, the abundances of species i and j should be positively correlated only if a'_{ih} and a'_{jh} have the same sign for all h (i.e., across rows in eq. [1]), or for all h where a'_{ih} and a'_{jh} are significantly large.

Spatial relationships among colonies of coexisting competitors are potentially of considerable significance among these relatively stationary, ground-nesting ants. Direct interference interactions are known to result in regular interspecific nest spacing (Davidson 1977*b*), and incorporation of indirect interspecific interactions introduces the potential for positive associations between colonies of two competing ant species under certain circumstances. If species h excludes species j from its nesting area and foraging grounds by exploitative or interference competition, a third species (i), which experiences intense competition from j but only a moderate amount from h, may be most likely to persist in close proximity to colonies of species h where K_j is locally increased. Thus, where competition occurs between species h and j, positive correlations may occur in the abundances of competitors i and h because of a positive a'_{ih}.

THE ANT COMMUNITY

This study was undertaken in the summer of 1974 in Chihuahuan Desert habitat near Rodeo, New Mexico. The principal ¼-ha study area contained seven common species of granivorous ants representing four genera of myrmicines. Indirect evidence (Davidson 1977*b*) suggests that these ant populations compete for food, and the results of experiments with removal of rodent competitors in nearby regions of the Sonoran Desert (Brown and Davidson 1977) also support the

contention that populations of desert seed-eating ants, in communities similar to that studied here, are food-limited. Adaptations such as hibernation, aestivation and seed storage help to smooth variability in the abundance of food resources. Although it is doubtful that this assemblage of harvester ants is in long-term evolutionary equilibrium with its environment, populations may actually approximate an equilibrium state with respect to their relatively short-term influences on one another.

METHODS

Exploitative Interactions

Ant diets and seed availability at the soil surface were sampled simultaneously twice during late summer and early fall of 1974, a season coinciding with maximum activity in these ants. (As used here, the term "seed" refers indiscriminately to both seeds and fruits found in ant diets and soil samples.) On each occasion, 30 ants from each of a number of colonies (see table 2) were robbed of their booty for laboratory determinations of diet composition. In general, the diets of replicate colonies of the same species showed remarkable consistency. Seventy-five soil samples (volume 10 cm × 10 cm × 1 cm deep) were taken by randomly positioning a soil sampling device in each of 75 25-m^2 quadrats during each of the two sampling periods. The seed content of these samples was analyzed later by flotation techniques similar to those outlined by Goodall et al. (1972). Most of the seeds were identified to species by comparison with plant specimens collected during seed set.

Based on characterization of the diets of six of seven ant species (*Solenopsis xyloni*, which forages on the surface approximately 1 mo [August] during each year was omitted), a matrix of exploitative interactions was constructed using Hurlbert's (1978) formulation:

$$a_{ij} = \frac{\sum_k (p_{ik}p_{jk}/f_k)}{\sum_k (p_{ik}^2/f_k)}. \qquad (2)$$

Here, p_{ik} is the proportionate numerical representation of the kth food type in the diet of the ith species, and f_k designates the relative abundance of food type k. It is widely recognized that large overlap values may be indicative of highly abundant, rather than limiting, resources. The Hurlbert index takes into account variation among resource states in abundance or availability, and permits unique and/or preferred resources to contribute disproportionately to the calculation of overlaps. Food types utilized by these harvester ants probably vary significantly in nutritional value and possibly also in toxin content. Although this nutritional heterogeneity can not be specified precisely, its effect on ant preferences and on the potential for competition can be incorporated into the overlap indices by discounting overlaps by resource availability, as in equation (2). The Hurlbert index is also intuitively satisfying because it is interpretable as the ratio of interspecific to intraspecific encounters (Hurlbert 1978).

Several clarifications should be made here regarding calculations of the parameters in equation (2). In all, 20 seed types (14 of them the seeds of annual plants) were utilized by the ants. Additional resource categories consisted of (1) vegetative material (largely unrecognizable), (2) termite larvae, and (3) other insect material. Termites were distinguished from other insects, because a distinctive searching behavior was employed by the ants in hunting them. Although the abundances of the seed types in the soils had been estimated directly from soil analyses, similar data were not available for vegetative material or termites and other insects. In addition, for three seed types not discovered in soil samples, f_k values equal to zero would have resulted in division by zero. The following procedure was adopted as a solution to both of these problems: For each resource category, relative availability was determined as the proportionate representation of the food type in the total sample of ant diets. This method of calculating the relative abundance of resources (the f_k in eq. [2]) produced f_k values that very precisely match the f_k values based on soil analyses for the 16 food types for which both measures were available (table 1). The somewhat surprisingly good correspondence in these comparisons has been confirmed independently by Robert Chew (unpublished data) for seeds and ants in a nearby creosote bush habitat. The remarkable fit between the seed production spectrum and the pattern of seed utilization by harvester ants probably reflects the fine-grained searching behavior of granivorous ants in combination with the displaced resource requirements of coexisting ant species (Davidson 1977*b*).

The calculations outlined above thus result in two overlap matrices representative of interspecific exploitative interactions for September and October, respectively. Corresponding elements of these two matrices were averaged to yield a single matrix. Throughout much of the remainder of 1974 some combination of climatic stress and lower resource availability resulted in significantly reduced ant activity levels (Davidson 1977*a*).

Interference Interactions

Any evaluation of the net effects of competition must surely incorporate interference as well as exploitative interactions. Although interference competition may generally predominate in ant communities (summarized in Wilson 1971), it appears to be relatively uncommon in interactions among desert ants over seeds. Only one such interaction, that between *Pogonomyrmex rugosus* and *P. desertorum* is expressed significantly in the six-species community studied here (Davidson 1977*b*). In order to incorporate the interference terms in the matrix of exploitative interaction coefficients, these terms must be expressed in a currency equivalent to that in which exploitative interactions are represented. Interference terms, expressed in the currency of resources, were calculated on the basis of bait turnovers involving the two species in four bait censuses; two at Rodeo, New Mexico and two at Deming, New Mexico. It is likely that each confrontation over a bait involved a single colony of each species, so that probabilities of bait control in areas of foraging overlap may be taken as per capita measures of interference

TABLE 1

COMPARED ESTIMATES OF RELATIVE RESOURCE ABUNDANCE BASED ON: *a*, SOIL SAMPLES; *b*, PROPORTIONATE USAGE BY THE TOTAL ANT COMMUNITY FOR SIXTEEN SEED TYPES IN SEPTEMBER AND OCTOBER, 1974

September		October	
a	*b*	*a*	*b*
.006	.007	.004	.004
.022	.002	.042	.042
.101	.085	.009	.009
.001	.001	.089	.090
.006	.007	.005	.005
.014	.014	.013	.012
.075	.076	.041	.040
.733	.743	.079	.079
.015	.026	.687	.684
.002	.003	.007	.008
.009	.001	.005	.005
.000	.009	.008	.008
.000	.004	.004	.004
.000	.004	.000	.003
.003	.004	.004	.004
.000	.003	.002	.003

competition. Both the larger size of *P. rugosus* workers (averaging 2.1 mm longer than those of *P. desertorum*) and their tendency to forage in groups may account for a disparity in the magnitude of the two interference coefficients. For 20 baits known to have been discovered by both species, 80% were controlled by *P. rugosus* and 20% were taken over by *P. desertorum*.

The manner in which these measures should be incorporated into the matrix of exploitative interactions is not straightforward. Interference probably precludes most exploitative competition between *P. rugosus* and *P. desertorum*. Mapping patterns of interspecific colony dispersion reveals that colonies of the two species are regularly spaced from one another (Davidson 1977*b*), and I have witnessed *P. rugosus* successfully interfering with nest-founding attempts by *P. desertorum*. During many hours of observing individually marked workers of the two species, I found that interspecific encounters invariably led to avoidance behavior or, more commonly, to active aggression, even in the absence of baits. Since both the probability of the two competitors simultaneously encountering resources and the probability of control of resources reflect the outcome of interference interactions, it may be appropriate simply to substitute measures of interference competition for the corresponding coefficients in the matrix of exploitative interactions.

While the 4:1 ratio was preserved in the experimentally derived interference terms, the values themselves were scaled upward in keeping with assumptions of the competition matrix. Ones on the diagonals of this matrix indicate that individuals of a given species are exact replacements for one another, as evaluated by resource utilization. Interspecific interaction coefficients must be understood in relationship to the unit intraspecific coefficients. In competition between two

individuals of a species, it is assumed that neither has an advantage and each has a 50% chance of winning the competition. Such is not the case in competition between *P. rugosus* and *P. desertorum*. The latter species has a greater than 50% chance of losing the competition. If a 50% chance of losing is designated by 1, losing at a frequency of 80% must correspond to a competition coefficient of 1.60, expressing the effect of *P. rugosus* on *P. desertorum*. By identical reasoning, a 20% chance of *P. desertorum* winning should translate to an interference coefficient of .40 as an estimate of the reciprocal interspecific interaction. These terms replace the values for the corresponding exploitative interactions in the competition matrix.

Empirical Tests

Tests for the correlation in species abundances predicted by the normalized inverse of the matrix of competitive interactions are based on censuses of colony abundances on 23 $\frac{1}{4}$-ha study plots, where experimental investigations of granivore communities were initiated in July and August of 1977. These plots, located within approximately 0.5–2.0 km of the original Rodeo, New Mexico study area, are separated from one another by a minimum distance of 25 m. For *Novomessor cockerelli* (E. André) and *Pogonomyrmex rugosus* Emery, two species with large and conspicuous nest sites, census figures represent actual colony numbers per $\frac{1}{4}$-ha plot plus one additional colony for every three colonies closely bordering the plot and likely to be foraging extensively on it. Colony counts for species with small, inconspicuous nest sites (*Pogonomyrmex desertorum* Wheeler, *Pheidole xerophila* Wheeler, and *Pheidole sitarches* Wheeler) are extrapolated from a sample of 49 circular quadrats of 2.0 m radius on each plot. Because the latter three species tended to forage over relatively short distances in comparison to *Pogonomyrmex rugosus* and *N. cockerelli* (generally < 5 m versus < 25–30 m in the latter two species), no colonies outside the plot boundaries were censused.

Finally, on several of the plots *Pogonomyrmex rugosus* is replaced by *Pogonomyrmex barbatus* (F. Smith), an ecological counterpart (Whitford et al. 1976; Davidson 1977*b*). *Pogonomyrmex rugosus* and *Pogonomyrmex barbatus* are characterized by similar worker body sizes, colony foraging behaviors, dietary preferences, and interference interactions with *Pogonomyrmex desertorum*. The two species are also interspecifically territorial (Hölldobler 1974; Whitford et al. 1976). The ecological likenesses between *Pogonomyrmex rugosus* and *Pogonomyrmex barbatus* should produce similar interspecific interactions with the other five granivore species; thus, no distinction was made between the two congeners in censusing the 23 plots.

RESULTS

The matrix of interspecific exploitative and interference interactions is given as table 2, and its normalized inverse (A') appears as table 3. As anticipated, not all of the $\partial \hat{N}_i / \partial K_j$ have the same sign; 11 of 30 coefficients are positive, indicating that

TABLE 2

MATRIX *A* OF EXPLOITATIVE AND INTERFERENCE INTERACTIONS

	NC	*PR*	*PD*	*HD*	*PX*	*PS*
Novomessor cockerelli (*NC*) $N = 5$†	1.00	.06*	.17	.46	.03	.04
Pogonomyrmex rugosus (*PR*) $N = 6$	.06	1.00	.40	.17	.05	.02
Pogonomyrmex desertorum (*PD*) $N = 10$	.21	1.60	1.00	.18	.23	.10
Pheidole desertorum (*HD*) $N = 4$	.44	.24	.19	1.00	.13	.22
Pheidole xerophila (*PX*) $N = 8$	.05	.07	.28	.15	1.00	.88
Pheidole sitarches (*PS*) $N = 5$	.05	.03	.11	.20	.75	1.00

* $\partial \hat{NC}/\partial \hat{PR}$.

† N = no. of colonies whose diets were sampled; varies directly with species abundances on the study plot.

TABLE 3

A', NORMALIZED INVERSE OF MATRIX *A*

	NC	*PR*	*PD*	*HD*	*PX*	*PS*
Novomessor cockerelli (*NC*)	1.00	.24*	−.12	−.52	.01	.03
Pogonomyrmex rugosus (*PR*)	.20	1.00	−.37	−.33	.06	−.01
Pogonomyrmex desertorum (*PD*)	−.49	−1.79	1.00	.50	−.27	.14
Pheidole desertorum (*HD*)	−.40	−.01	−.05	1.00	.06	−.14
Pheidole xerophila (*PX*)	.19	.83	−.49	−.14	1.00	−.90
Pheidole sitarches (*PS*)	−.06	−.47	.29	−.11	−.74	1.00

* $\partial \hat{NC}/\partial K_{PR}$.

enhancement of K_j should lead to an increase in the equilibrium density of $\hat{N}_i$, in the context of all the interactions in the six-species assemblage.

Based on the signs of the coefficients in table 3, correlations in species abundances can be projected for several species-pairs. The matrix predicts that the abundance of *Pogonomyrmex rugosus* should be positively correlated with the abundances of *Pheidole xerophila* and *Novomessor cockerelli*. Corresponding row elements of *Pogonomyrmex rugosus* and *Pheidole xerophila* have identical signs over all the columns of A', indicating that the two species share qualitatively similar responses to variations in each of the six K's. The equivalent result obtains in the comparison between *Pogonomyrmex rugosus* and *N. cockerelli*, with the single exception of coefficients in column 6. The absolute values of these two

elements are very small in relationship to the absolute values of other coefficients in the same rows. Unless variations in the carrying capacity of *Pheidole sitarches* are of consistently much greater amplitude than variations in the other five K's, the abundances of *Pogonomyrmex rugosus* and *N. cockerelli* should be positively related. In two additional comparisons (*NC-PX* and *PD-PS*) pairs of species have their corresponding row elements similarly signed over five of six columns of A', but in each of these cases at least one of the coefficients in the exceptional column is notably large. Corresponding row coefficients are consistently opposite in sign for two pairs of species (*PD-PX* and *PR-PD*). Because members of these species pairs have qualitatively different responses to variations in each of the six K's, their abundances should be negatively correlated.

Empirical support exists for all four of the projected interspecific relationships. Table 4 compares the predicted correlations in colony abundances with the positive and negative interspecific associations measured on the 23 ¼-ha study plots; three of these correlations are significant and in the anticipated directions. The remaining comparison is between two species (*NC* and *PR*) whose numbers are relatively low on all plots. Alternative evidence for the hypothesized positive association between *N. cockerelli* and *Pogonomyrmex rugosus* exists in the pattern of the interspecific colony dispersion on the original (1974) study plot (fig. 1). Only three mature colonies of each of these two species occupy this ¼-ha area, and the nearest neighbor of each of these six colonies is a colony of the opposite species. Although this result is significant ($P < .05$) in the binomial test, it does not specify whether the pattern results primarily from negative intraspecific interactions or from net interspecific facilitation. The two colonies of each species located nearest the mapped plot also occur in closely associated (within 6.5 m) interspecific pairs, one pair immediately to the southwest and another at a some-

TABLE 4

TESTS FOR HYPOTHESIZED CORRELATIONS AND PROMINENT PATHWAYS RESPONSIBLE FOR CORRELATIONS

Species Pair	Predicted Correlation	Observed Correlation, $P <$	Prominent Interaction(s)	Major Pathway(s)
PD-PX	−	−, .05	$\frac{\partial \hat{PD}, \partial \hat{PX}}{\partial K_{PR}}$	$PR \rightarrow PD \rightarrow PX$
PR-PD	−	−, .01	$\frac{\partial \hat{PD}, \partial \hat{PR}}{\partial K_{PR}}$	Direct effects
PR-PX	+	+, .01	$\frac{\partial \hat{PX}, \partial \hat{PR}}{\partial K_{PR}}$	$PR \rightarrow PD \rightarrow PX$
PR-NC	+	+, NS	$\frac{\partial \hat{PR}, \partial \hat{NC}}{\partial K_{PR}}$ and $\frac{\partial \hat{PR}, \partial \hat{NC}}{\partial K_{NC}}$	$PR \rightarrow PD \rightarrow NC$ and $NC \rightarrow PD \rightarrow PR$

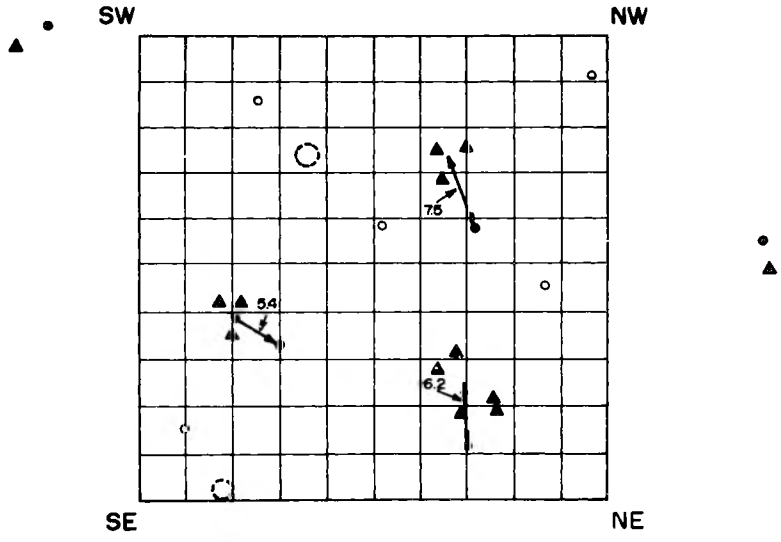

FIG. 1.—Colonies of *Pogonomyrmex rugosus* (solid circles) and *Novomessor cockerelli* (triangles) mapped in August, 1974, on a ¼-ha plot near Rodeo, New Mexico. Dotted circles specify the positions of incipient colonies of *N. cockerelli* that had failed by 1975. All of the remaining colonies have persisted from 1974 until now. Positions of colonies outside the demarcated area are only known approximately. Colonies of *N. cockerelli* are polydomous, and clusters of triangles represent multiple nest entrances of single colonies.

what greater distance to the north. This remarkable association between colonies of the two species appears to be based on something more than negative intraspecific interactions.

Table 4 also identifies the pairs of coefficients in A' that appear to contribute most prominently to the observed species-abundance relationships by virtue of the large absolute values characterizing both members of the pair. The major pathways contributing to the prominence of such interactions may then be ascertained by inspection from table 2. For example, the projected dramatic and opposite responses of PD and PX to changes in the carrying capacity of PR (table 3) are probably the most significant determinants of the negative association between the former two species. Table 2 reveals the nature of interspecific interaction pathway involved here. *Pogonomyrmex rugosus* interferes intensively with *Pogonomyrmex desertorum,* which in turn competes exploitatively with *Pheidole xerophila.* On the other hand, the negatively correlated abundances of *Pogonomyrmex desertorum* and *Pogonomyrmex rugosus* are explained largely by direct interference competition between these two species; that is, the exceptional magnitudes of $\partial \hat{PD}/\partial K_{PR}$ and $\partial \hat{PR}/\partial K_{PD}$ simply reflect the similarly high values of $\partial \hat{PD}/\partial \hat{PR}$ and $\partial \hat{PR}/\partial \hat{PD}$ in matrix A (table 2). Responses to fluctuations in the carrying capacity of *Pogonomyrmex rugosus* appear to figure prominently in both of the positive interspecific associations shown in table 4. In each case, the major contributing interaction pathway involves indirect facilitation of species (*NC* and

PX) with which *PD* competes exploitatively, mediated by the strong interference effect of *PR* on *PD*.

DISCUSSION

Considerable disillusionment has been expressed with simple linear models of competition (Wilbur 1972; Preston 1973; Neill 1974). The research presented here illustrates that such models can generate predictions that correspond at least qualitatively to reality in one competitively structured species assemblage for which diffuse interactions can be modeled explicitly. Discounting overlaps by resource abundance, incorporating interference as well as exploitative competition, and taking into account indirect as well as direct interaction pathways have all contributed to the accuracy with which interspecific interactions could be estimated. Although the precise values of interaction coefficients cannot be taken literally, the general form of the interaction matrix probably accords relatively well with the actual structure of interactions in this six species assemblage, and this structure is sufficient to define probable species abundance relationships. A second factor potentially contributing to successful prediction of species abundance patterns is that the majority of the interspecific competitive interactions are exploitative. Though no firm evidence substantiates this hypothesis, it is intuitively reasonable that the net effects of exploitative competition are less likely than those of interference competition to be nonlinear. For example, in direct interference confrontations, the presence of a third species may alter the behaviors of one or both of two competitors in a manner that can not be predicted from a linear model. Though this is probably true to some extent for exploitative competition as well, significant nonlinearities may be less likely where interactions are principally exploitative.

Unique characteristics of the consumer-resource system studied here have facilitated the analysis of exploitative competition. Seeds are discrete resources whose abundances are relatively easy to quantify. With some justification, studies of resource overlap may be limited to the single resource dimension of food. Traditionally, resource allocation based on microhabitat or temporal partitioning is also evaluated and, depending on the degree of interrelationship of these dimensions, summation or product overlaps are calculated. Among the desert harvester ants, resource allocation appears to be based primarily on particle size and density distribution (Davidson 1977*a*, 1977*b*); both characteristics are highly specific to a given resource taxon (D. W. Davidson, unpublished data). There is little evidence to indicate that either microhabitat or temporal partitioning on a diurnal time scale promote coexistence in the ant community studied here. Using three distinct analysis techniques to evaluate interspecific patterns of colony dispersion and foraging area overlap, both in the presence and absence of baits, I was able to discern spatial separation for only two species-pairs, *Pogonomyrmex rugosus* and *Pogonomyrmex desertorum,* and the latter species and *P. barbatus* (Davidson 1977*b*). In each case, the spatial separation appears to represent interspecific territorial defense, rather than allocation of space according to mi-

crohabitat preferenda. This important interference component of competition is incorporated into the matrix of competitive interactions in table 2. While interspecific differences were apparent in the diurnal activity schedules of these ants, temporal foraging overlaps were extensive. The intermittent nature of seed renewal in these habitats (once or twice annually) would seem to preclude resource allocation by temporal partitioning on all but a seasonal time scale. Thus, it is possible to reduce the exploitative interactions in this species assemblage to a single dimension and avoid many of the difficulties (May 1975) associated with choosing between additive and multiplicative overlaps.

The detailed investigation of this harvester ant community illustrates that the abundances of competitors may be positively correlated if the species' population growth rates respond similarly to fluctuations in the carrying capacities of all species in the assemblage of closely interacting competitors. It appears also that a few major indirect interaction pathways, made prominent by relatively intense direct interactions among component species, are of primary importance in accounting for positive associations among competitors. The predicted positive correlations in the abundances of *Pogonomyrmex rugosus* and *N. cockerelli* and *Pogonomyrmex rugosus* and *Pheidole xerophila* hinge predominantly on the strong direct interference effect of *Pogonomyrmex rugosus* on *Pogonomyrmex desertorum,* a species that interacts negatively with *N. cockerelli* and *Pheidole xerophila* through direct exploitative competition. The significance of this indirect pathway is especially apparent in the context of data on colony dispersion. By excluding *Pogonomyrmex desertorum* from nesting sites and foraging grounds, colonies of *Pogonomyrmex rugosus* may provide locally favorable habitats for *N. cockerelli.* Resources shared by *Pogonomyrmex desertorum* and *N. cockerelli* but not exploited by *Pogonomyrmex rugosus* would be locally more abundant near colonies of the latter species. On the major $\frac{1}{4}$-ha study plot, the two colonies of *N. cockerelli* that disappeared over a 2-yr period were the only two colonies not spatially associated with *Pogonomyrmex rugosus* mounds (fig. 1). The importance of this indirect pathway was undertaken in July of 1977 by analyzing interspecific colony spacing in four similar habitats where *Pogonomyrmex desertorum* was rare or absent, but where the existing assemblage of harvester ants otherwise resembled the group studied in 1974. In the five-species A' matrix with *Pogonomyrmex desertorum* omitted, the net positive interactions between *Pogonomyrmex rugosus* and *N. cockerelli* are substantially reduced ($\partial \hat{PR}/\partial K_{NC} = .02$ and $\partial \hat{NC}/\partial K_{PR} = .07$), while corresponding row coefficients for the two species remain similarly signed across all columns of the matrix. If the "apparent facilitation" of *N. cockerelli* by *Pogonomyrmex rugosus* is primarily responsible for the positive spatial association between these two species, colonies ought not to show interspecific association where *Pogonomyrmex desertorum* is rare or absent. This is precisely the pattern observed, as illustrated in figure 2.

An obvious alternative to interpreting the above data in the context of net competitive interactions is to invoke interspecific differences in fitness over slightly different habitats or microhabitats. Although the 23 plots differ to some extent in the number and species composition of perennial plants (here dominated by *Ephedra trifurca, Fluorensia cerna* and *Gutierresia* sp.), none of these differ-

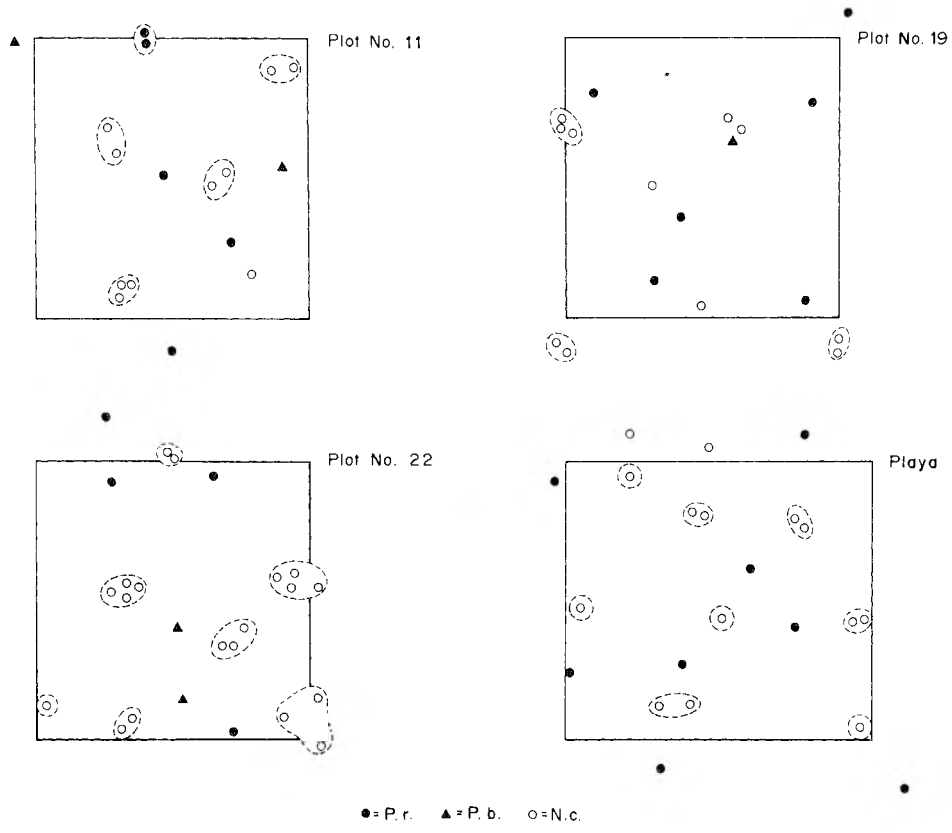

FIG. 2.—Colonies of *Pogonomyrmex rugosus* (or its ecological counterpart *P. barbatus*) and *Novomessor cockerelli* mapped in July, 1977, on four plots where *Pogonomyrmex desertorum* was rare or absent.

ences appear to account for the positive and negative associations of species documented in table 3 and figure 1. Because the composition of the annual plant community varies spatially from year to year, and ant colonies persist over a number of years, habitat selection with respect to these plants is unlikely. However, it is impossible to rule out habitat selection with reference to some subtle, unmeasured habitat feature, and experiments currently in progress may help to differentiate between the hypotheses of diffuse competition and habitat selection as explanations for positive associations among competitors.

The potential for apparent facilitation between species that compete directly for resources should characterize all assemblages of three or more competitors (Levins 1975; Levine 1976). As Holt (1977) has recently cautioned, diffuse interactions may complicate analyses of interspecific interactions whether these analyses are based on the interpretation of static patterns in species abundances or population responses to experimental manipulation of population densities or limiting resources. Experimental studies of population interactions seldom are sufficiently well-controlled to detect whether responses to manipulations reflect direct pair-

wise interspecific interactions or apparent interactions as modified by other elements of the community.

SUMMARY

Exploitative and interference competition are investigated in detail in a community of six coexisting species of granivorous desert ants. A linear model that includes both direct and indirect competitive interactions is used to predict positive or negative correlations in the abundances of competitors. Data on the abundances of the six ant species on 23 ¼-ha plots provide empirical support for the four predictions so generated. "Apparent facilitation," in the form of positive interspecific spatial associations of colonies, is detected between two competitors and interpreted as arising from indirect pathways of interspecific interaction. The results illustrate how indirect interactions among species at a single trophic level may play a significant role in organizing natural communities.

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